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Some properties of the aggregations of soil arthropods: *Cryptostigmata*

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(Accepted: 2. 1. 1975)

Contents

1. Introduction	355
2. Techniques of statistical analysis.	356
3. Results	357
3.1. Data transformation; 3.2. Spatial distribution; 3.3. The effect of seasonal distribution	
4. Discussion	360
5. Summary · Zusammenfassung	362
6. Acknowledgements.	362
7. References	362

1. Introduction

In reviewing aspects of the distribution of soil arthropods, BUTCHER et al. (1971) show that in the majority of studies of Collembola and Cryptostigmata there is an aggregated distribution of individuals within the three-dimensional environment of the soil. They conclude that the aggregation tendencies can be attributed to "water, temperature, time of day, microclimate, season, food source, microflora, vegetation, clustering of eggs, . . ." and the "reliability of each of these influences depend in part upon the extent to which individual investigators have sought to document their speculations, inferences or conclusions".

Sampling of these aggregated populations poses several problems. First, since the variability of numbers of individuals per sample is large, a very large series of samples will be required for accurate estimates of the mean population density or for comparing population densities between habitats or between seasons. However, the large number of samples poses the problems of handling the samples and of identifying and counting the arthropods. More importantly, if the object is to determine the relation between number of arthropods and some environmental factor or factors, often presumed to be the influences acting directly to cause the aggregating tendency, then a large series of random samples would be likely to be the most efficient sampling procedure. If, however, one is interested in investigating the aggregation tendency *per se*, then a large number of systematically selected samples is the most efficient sampling procedure. But, long series of contiguous samples, although efficient for investigating the nature of aggregations, are inefficient both for determining mean population densities and for making comparisons.

The sampling procedure used in this study, as previously described by USHER (1969, 1971a), consisted of taking two sets of 48 contiguous samples on each of twelve occasions during a year. The samples were cut from the soil by a tool consisting of sharp stainless steel blades cutting 16 square cores, each of side 4 cm, arranged in a square of 4 rows and 4 columns. Each core was cut into three layers, each 1 cm thick, so that only the surface 3 cm of the soil profile were being used. Preliminary sampling had shown that at least 95 per cent of the Cryptostigmata occurred in this zone of the soil.

The site selected for these studies was part of a semi-natural Scots pine forest (*Pinus sylvestris* L. ssp. *scotica* (SCHOTT) E. F. WARBURG) on Cnoc Eoghainn in the Black Wood of Rannoch, Perthshire, Scotland (56°38' N, 4°22' W; Nat. Grid Ref. NN 551546). The climate is cold and moist with an average annual precipitation of approximately 1200 mm and a mean annual temperature of 6 °C. The site, its climate, geology and pedology, and the methods of sampling and extraction of arthropods from the samples have been described by USHER (1967). The Collembola of the site have been described (USHER 1969, 1970a), as have the Mesostigmata (USHER 1971a, 1971b) and the micro-environment (USHER 1970b).

2. Techniques of Statistical Analysis

A property of the Poisson or random distribution is that the variance, σ^2 , and mean, μ , are equal. In sampling, it is taken that the sample estimates of the parameters, s^2 and m respectively, are not significantly different from each other. Following BLISS and FISHER (1953) and HEALY (1962) it is appropriate to test for equality by

$$\chi^2 = \frac{s^2}{m} (n - 1) \quad (1)$$

where χ^2 has $(n - 1)$ degrees of freedom. This test is only totally appropriate if the samples were collected randomly, since in a series of contiguous quadrats several of the large counts could be clustered together. Such an aggregation would be shown as a gradient in numbers of mites either across rows or columns or both. The following procedure was thus used.

The first analysis was an analysis of variance separating out the effects of rows and columns. If either or both was significant the set of samples was recorded as showing a gradient form of aggregation (see, for example, the analysis of *Friesia mirabilis* in USHER 1969). If both row and column effects were non-significant, the χ^2 criterion in equation (1) was calculated. If this was significantly smaller than expectation ($p > 0.95$) then the distribution was taken to be uniform. If, however, χ^2 was significantly larger than expectation ($p < 0.05$) then the species was considered to be aggregated. With nonsignificant values of χ^2 the distribution was assumed to be random. Aggregated distributions could be separated into two types; those that on visual inspection showed distinct aggregations and those in which no distinct aggregations could be seen. If distinct aggregations could be seen, the analysis proceeded by empirically locating aggregations, eliminating them from the data, and testing the residual distribution by the χ^2 criterion in equation (1). The procedure of locating and eliminating aggregations was terminated when the residual distribution could be taken as being random. The procedure is illustrated for *Isotoma sensibilis* by USHER (1969).

Table 1. The species of Cryptostigmata included in the analyses with their abundance

Species	Number collected	Maximum number collected on any one sampling date
<i>Nanhermannia nana</i> (NICOLET)	800	184
<i>Camisia spinifer</i> (C. L. KOCH)	698	171
<i>C. segnis</i> (HERMANN)	38	11
<i>Platynothrus peltifer</i> (C. L. KOCH)	3,285	705
<i>Porobelba spinosa</i> (SELLNICK)	670	113
<i>Oribella lanceolata</i> (MICHAEL)	708	266
<i>Ceratoppia bipilis</i> (HERMANN)	1,406	208
<i>Tectocephus velatus</i> (MICHAEL)	12,165	1,625
<i>Cepheus dentatus</i> (MICHAEL)	95	15
<i>Adoristes poppei</i> (OUDEMANS)	1,358	161
<i>Chamobates schülzi</i> (OUDEMANS)	888	172
<i>Eupelops</i> spp.	707	95
<i>Steganacarus magnus</i> (NICOLET)	2,784	430
<i>Phthiracarus piger</i> (SCOPOLI)	589	84
Total	26,191	—

Note: The nomenclature follows WILLMANN (1931), with later generic revisions.

3. Results

3.0. Prefatory note

Counts were made on the 14 most commonly occurring species of Cryptostigmata (see table 1). As a criterion for sufficiency of data, only those blocks of samples that had a mean population density of at least 0.5 individuals per sample (24 individuals in the block of samples) were used in the analyses. It will be seen from table 1 that *C. segnis* and *C. dentatus* were always too infrequent for analyses to be carried out on their aggregations. *S. magnus* was the only species to be sufficiently frequent for analyses to be performed on all 24 sets of data.

3.1. Data transformation

In biological studies it is frequently a problem to decide on a suitable form of data transformation to use so that normal statistical tests, based on the normal distribution, can be applied. A general form of transformation has been proposed (Box and Cox 1964), but this is difficult to apply and the parameters of the transformation can only be determined by a complicated iterative procedure. A transformation based on the general applicability of the negative binomial distribution to Cryptostigmata data (HARTENSTEIN 1961), using the parameters of this distribution, has been proposed by GÉRARD and BERTHET (1966). However, using many studies on different groups of arthropods, TAYLOR (1961) proposed that the variance was related to a fractional power of the mean, thus

$$s^2 = am^b \quad (2)$$

where a and b are constants and where

$$k = 1 - b/2 \quad (3)$$

defines a transformation of the form

$$x' = x^k$$

where k is defined by equation (3), x is the number of a species in a sample, and x' is the transformed variable. The constants a and b in equation (2) can be estimated by regression analysis of the logarithm of s^2 on the logarithm of m . Tables of the transformation have been published (HEALY and TAYLOR 1962).

The data for the 14 species of Cryptostigmata are shown in Table 2. The values of b lie between 1.12 and 1.70, in general rather larger than those observed with the Mesostigmata (USHER 1971a). The magnitude of these b values supports the hypothesis that the tendency to aggregate is stronger in the humus feeding and non-predatory mites.

Table 2. The parameters of Taylor's relation between the variance and the mean ($s^2 = am^b$) where a and b are estimated by regression analysis and r is the correlation between the logarithms of s^2 and the logarithm of m , with the sample size in brackets

Species	Value of a	Value of b	Value of r	Value of k
<i>N. nana</i>	1.845	1.236	0.991 (22)	0.32
<i>C. spinifer</i>	2.131	1.298	0.969 (24)	0.35
<i>C. segnis</i>	1.432	1.122	0.979 (13)	0.44
<i>P. peltifer</i>				
juveniles	1.840	1.429	0.966 (24)	0.28
adults	1.671	1.478	0.978 (24)	0.26
<i>P. spinosa</i>	1.749	1.240	0.959 (24)	0.38
<i>O. lanceolata</i>	1.851	1.284	0.980 (22)	0.36
<i>C. bipilis</i>				
juveniles	2.705	1.356	0.938 (24)	0.32
adults	3.125	1.698	0.919 (24)	0.15
<i>T. velatus</i>	1.732	1.571	0.956 (24)	0.21
<i>C. dentatus</i>	1.428	1.105	0.960 (23)	0.45
<i>A. poppei</i>	2.366	1.623	0.857 (24)	0.19
<i>C. schülzi</i>	1.476	1.146	0.933 (24)	0.43
<i>Eupelops</i> spp.	2.294	1.378	0.840 (24)	0.31
<i>S. magnus</i>	1.616	1.556	0.928 (24)	0.22
<i>P. piger</i>	1.530	1.149	0.984 (24)	0.43

Note: Values of k are obtained by the formula given by HEALY and TAYLOR (1962), and indicate a power transformation of the form $x' = x^k$, where x' is the transformed variable.

3.2. Spatial distribution

A total of 212 analyses have been performed on the data of 12 species (table 3), though the adult and juvenile stages of *C. bipilis* and *P. peltifer* have been kept separate in the analyses. The analysis of variance, performed on all the data, indicated that gradients occurred in 48 sets of data. None of the species showed this form of aggregation to the exclusion of other aggregated distributions. The χ^2 criterion, equation (1), indicated that no species showed an uniform distribution, and that random distributions only occurred in 17 (8.0 per cent) of the blocks of samples. Of the 147 sets of data that showed a significant χ^2 value, distinct aggregations could be seen in 99 leaving 48 that had to be assigned to the "other aggregations" group. In this group *T. velatus* and *S. magnus* are the most frequently occurring species, always occurring here at times of high population density. It therefore seems likely that the analysis was unable to locate aggregations since the sample size was too large compared with the aggregation size, particularly for *T. velatus* which is a very small species of mite.

Table 3. A summary of the distributions and aggregation types for all species of Cryptostigmata that occurred within a block of samples with an average frequency of 0.5 or more individuals per sample

Species	Total number of blocks	Uniform distribution	Random distribution	Aggregated distributions		
				Gradients	Distinct aggregations	Other
<i>N. nana</i>	8	0	0	2	5	1
<i>C. spinifer</i>	12	0	0	2	7	3
<i>P. peltifer</i>						
juveniles	17	0	1	3	10	3
adults	18	0	3	4	8	3
<i>P. spinosa</i>	12	0	2	2	8	0
<i>O. lanceolata</i>	8	0	2	1	5	0
<i>C. bipilis</i>						
juveniles	10	0	0	2	6	2
adults	18	0	1	3	14	0
<i>T. velatus</i>	23	0	0	9	0	14
<i>A. poppei</i>	23	0	2	2	11	8
<i>C. schützi</i>	13	0	2	3	7	1
<i>Eupelops</i> pp.	15	0	2	4	8	1
<i>S. magnus</i>	24	0	0	9	5	10
<i>P. piger</i>	11	0	2	2	5	2
Total	212	0	17	48	99	48

Table 4. The frequencies with which numbers of aggregations occurred in the blocks of samples, and the mean number of aggregations per block

Species	Number of aggregations in a block					Mean
	1	2	3	4	5	
<i>N. nana</i>	4	1	0	0	0	1.20
<i>C. spinifer</i>	3	3	1	0	0	1.71
<i>P. peltifer</i>						
juveniles	2	6	2	0	0	2.00
adults	2	3	0	1	2	2.75
<i>P. spinosa</i>	2	3	1	2	0	2.38
<i>O. lanceolata</i>	1	1	3	0	0	2.40
<i>C. bipilis</i>						
juveniles	1	3	2	0	0	2.17
adults	2	5	6	1	0	2.43
<i>A. poppei</i>	1	2	3	4	1	3.18
<i>C. schützi</i>	7	0	0	0	0	1.00
<i>Eupelops</i> spp.	3	3	0	2	0	2.12
<i>S. magnus</i>	2	2	0	1	0	2.00
<i>P. piger</i>	3	2	0	0	0	1.40
Total	33	34	18	11	3	2.16

Note: The data are derived from the 'distinct aggregations' column of Table 3.

In blocks of samples where distinct aggregations could be seen the numbers of aggregations per block are shown in Table 4. Approximately equal numbers of blocks showed one, two and three or more aggregations, giving an overall mean for the Cryptostigmata of 2.16 aggregations per block. This figure can be compared with 1.95 and 2.94 for the Mesostigmata and Collembola respectively. Some species, for example *C. schützi* and *N. nana*, showed a consistently small number of aggregations per block of samples, and together with the occurrence of gradients, indicate that aggregations are widely separated. In the Collembola it was found that the mean number of aggregations of adults per block of samples was smaller than the mean number of juveniles. In the Cryptostigmata, although it might appear that the mean number of aggregations of adult *C. bipilis* and *P. peltifer* is greater than the mean of the juveniles, the differences are not significant ($t = 0.646$ and 1.305 respectively).

3.3. The effects of seasonal distribution

Some species of Mesostigmata showed a seasonal trend in the nature of their distribution in the soil (USHER 1971a). The seasonal influences on the Cryptostigmata populations (USHER 1975) generally show a single population maximum in the year, and in some species this can be related to the nature of the aggregations.

P. peltifer showed a relatively large proportion of juvenile stages (a mean of more than 50 per cent) during the winter, from September to April. During this period of the year distinct aggregations could usually be detected, generally with 2 aggregations per block. During the summer when the population density of juveniles was smaller a variety of distributions was observed, both random and aggregated with gradients and distinct aggregations. There was, however, no seasonal influence on the distribution of the adults of this species. A very similar seasonal influence is shown by *C. bipilis* where the maximum percentage of juveniles occurred in the late summer and autumn. All of the distinct aggregations recorded in table 3 occurred during this period of the year, the other forms of distribution occurring between December and May. The adults, however, showed distinct aggregations throughout the year though there are apparently more during the winter (September to March) than during the summer (the means are 2.8 and 1.8 aggregations per block of samples respectively). In these two species distinct aggregations occur at the season of maximum population density. A similar pattern is shown by *C. schützi* and *O. lanceolata* which have maximum population densities during the winter, at which time distinct aggregations can be seen.

The two species *S. magnus* and *P. piger* show a different seasonal effect. A minimum population density of *S. magnus* was recorded between December and May, and it is only during this period of the year that distinct aggregations could be seen. During the remainder of the year the nature of the aggregations was not clear and they are recorded in the "other aggregated distributions" column in table 3. Gradients across the block of samples were demonstrated during all seasons of the year. Distinct aggregations of *P. piger* also occurred only between December and March whilst at other times of the year gradients or other aggregated distributions were found. This winter period also coincides with the period of minimum population density of this species.

A third type of seasonal effect is shown by *C. spinifer*. The population density was increasing between November and February, during which period distinct aggregations could be seen. The number of aggregations in a block increased from one to three over this period. In June the population density was decreasing and again distinct aggregations could be seen. Between February and June the distribution, although aggregated, was neither in distinct aggregations nor gradients. After June until the autumn the species was too infrequent for analysis, but in the autumn, just at the start of the population increase, gradients could be seen in the data.

The aggregations of *P. spinosa* are intermediate between those of the first and third groups previously described. USHER (1975) indicates that this species might have two population maxima, one in the winter and another in the late summer. Distinct aggregations could be seen in the data during the winter population maximum and during the summer

when the population was increasing. During the late summer maximum population and continuing into the autumn either gradients or a random distribution were indicated. The other species included in table 3, *A. poppei*, *N. nana*, *T. velatus* and *Pelops* spp. show no relation between aggregation and seasonal abundance of the species.

4. Discussion

The data in table 3 demonstrate that it is normal for the Cryptostigmata to have an aggregated distribution within the soil. Although such forms of distribution are frequent within all groups of soil arthropods, it is particularly strongly developed in the Cryptostigmata (table 5). This is likely to be due to two facets of the mites themselves. First, the Mesostigmata show a relatively large percentage of random distributions, and USHER (1971a) speculated that this was due to the predatory nature of many of the species. The Mesostigmata will be searching in the soil for prey, and are thus less likely to aggregate in areas of particularly favourable micro-environmental conditions. None of the Cryptostigmata recorded in table 1 is known to be a predator. Secondly, the Collembola are able to move quickly and over relatively large distances. Although in some species the furcula is reduced, in many it is still developed and can be used extremely quickly. The actual act of cutting a contiguous set of samples takes a few seconds, and although precautions were taken it is likely that during the sampling process, some Collembola could have moved. The Cryptostigmata are not able to move quickly, and their defence mechanism consists more of the strength of their cuticle than an ability to escape. The speed of movement of the majority of species of Cryptostigmata is unknown, though BERTHE (1964) recorded maximum displacements of only 5–6 cm per day with *S. magnus* and 6–8 cm per day with *Xenillus tegeocramus*.

The Cryptostigmata thus demonstrate a high degree of aggregation. The nature of the aggregations has been considered by USHER (1969, 1971a) who distinguished three types which depend upon the population density and the response to forming aggregation. If r_n represents the correlation between the population density and the number of aggregations per unit volume, and r_s the correlation between the population density and the mean number of mites per aggregation, then types I, II and III can be defined by:

I, as the population density increases so does the number of aggregations, and thus r_n is positive and significant. Since the increasing population density is wholly reflected in more aggregations being formed it is likely that r_s would be non-significant.

II, as the population density increases so does the number of mites within an aggregation, and thus r_s is positive and significant. Since the increasing population density is wholly reflected in the size of individual aggregations it is likely that r_n would be non-significant.

III, as the population density increases so do both the number and size of the aggregations, and thus both r_n and r_s are likely to be positive and significant.

These three types of aggregations do not account for all combinations of significance of r_n and r_s , but it is likely that they can be explained in terms of the ecological niches of the arthropod species. A type I aggregation, which is possibly indicated by *C. spinifer* (table 6), would imply that the width of the species niche was quite wide, and hence that there was perhaps little difficulty in finding new locations to act as foci for new aggregations. With the Collembola it was suggested that this type of aggregation could reflect some fixed attribute of a species such as the location of an egg cluster, and hence that the foci were not directly chosen by the arthropods that formed the aggregations. However, a type II aggregation might imply a narrower niche width since more arthropods are crowding into the aggregations. This form of distribution is shown by *P. spinosa*, *A. poppei*, *P. piger*, *C. bipilis* adults and possibly by *O. lanceolata*. Following these arguments on type I and II aggregations, a type III aggregation would indicate a species with a wider species niche, but not too wide. Some of the increase in population is absorbed by increasing the number of individuals in the existing aggregations whilst there is also a response in founding new aggregations. *P. peltifer*, both adults and juveniles, is the only species to exhibit a type III aggregation (table 6).

Table 5. A comparison of the forms of distribution of soil arthropods in a Scots pine forest soil

	Cryptostigmata	Mesostigmata	Collembola
Number of sets of data analysed	212	118	234
Number of species, groups or life stages	14	12	16
Percentage of analyses with:			
(i) Uniform distribution	0	0	0.9
(ii) Random distribution	8.0	39.0	27.4
(iii) Aggregated distribution	92.0	61.0	71.7

Note: The data for the Cryptostigmata are taken from Table 3, for the Mesostigmata from USHER (1971a) and for the Collembola from USHER (1969). The aggregated distributions include gradients, distinct aggregations and others.

Table 6. The correlation between the number of a species of Cryptostigmata in the block of samples and either the number of aggregations in the block (r_n) or the mean number of that species within an aggregation (r_s)

Species	Degrees of freedom	r_n	Probability	r_s	Probability
		Correlation coefficient		Correlation coefficient	
<i>N. nana</i>	3	0.197	n.s.	0.731	n.s.
<i>C. spinifer</i>	5	0.683	+	0.488	n.s.
<i>P. peltifer</i>					
juveniles	8	0.788	**	0.583	+
adults	6	0.840	**	0.849	**
<i>P. spinosa</i>	6	0.204	n.s.	0.715	*
<i>O. lanceolata</i>	3	0.660	n.s.	0.839	+
<i>C. bipilis</i>					
juveniles	4	0.367	n.s.	-0.155	n.s.
adults	12	0.177	n.s.	0.713	**
<i>A. poppei</i>	9	-0.168	n.s.	0.776	**
<i>C. schultzi</i>	5	—	—	0.553	n.s.
<i>Eupelops</i> ssp.	6	0.390	n.s.	0.400	n.s.
<i>S. magnus</i>	3	-0.339	n.s.	0.728	n.s.
<i>P. piger</i>	3	0.080	n.s.	0.939	*

Note: In the probability columns n.s. denotes $p > 0.10$, + denotes $0.10 \geq p > 0.05$, * denotes $0.05 \geq p > 0.01$ and ** denotes $0.01 \geq p > 0.001$.

An interesting comparison can be drawn between the Cryptostigmata, Mesostigmata and Collembola of this habitat. The Mesostigmata (table 5) showed the least tendency towards an aggregated distribution, and they show the least tendency towards fitting into any of the three types of aggregation (USHER 1971a). The two groups that show any significant correlation, *Parazercon radiatus* and the unidentified juveniles, both exhibit type I aggregations.

Five species of Collembola have type I aggregations (USHER 1969) whilst none of the other species have type II or type III aggregations, unless non-significance of both r_n and r_s can be taken to imply a type III aggregation. Thus, whereas the Collembola and Mesostigmata tend to form type I aggregations the Cryptostigmata tend to form type II aggregations. The Cryptostigmata are thus showing the greatest tendency to aggregate and are also showing the narrowest of niche widths. Such a conclusion might appear as a paradox since some species of Cryptostigmata have extensive geographical distributions. Of the species listed in table 1, WALLWORK (1967) records *T. velatus*, *P. peltifer* and *C. bipilis* as occurring in both the New and the Old Worlds of the North Temperate region and both *T. velatus* and *P. peltifer* also occur in the Southern Temperate region (McMILLAN 1969, gives New Zealand records). However, WALLWORK (1967) shows that even those species that have wide geographical distributions "are not ubiquitous in the sense that they occur

in every type of soil throughout their geographical range", and that there may be critical factors of the environment, particularly soil moisture, that influence their distribution. The majority of species of Cryptostigmata show much more limited distributions, and indeed WALLWORK's examples from forest soils and adjacent pastures under different management regimes indicate that many species are likely to have relatively narrow niche widths.

5. Summary · Zusammenfassung

The population structure of 14 species of Cryptostigmata, occurring in a pine forest soil in Scotland, was studied for one year. It was found that all species had a strong tendency to aggregated distributions, this tendency being greater in the Cryptostigmata than in the other groups of microarthropods that occurred in the same habitat. Some species show seasonal differences in the form of their aggregations. A study of the correlation between population density and either the number of aggregations or the density of mites in the aggregation reveals three types of distribution in the Cryptostigmata. A type I aggregation, exhibited by *Camisia spinifer*, indicates that the number of aggregations increases with the population density. Type II aggregations, exhibited by *Porobelba spinosa*, *Adoristes poppei*, *Phthiracarus piger*, adults of *Ceratoppia bipilis* and *Oribella lanceolata* indicate that the density of mites within aggregations increases with population density. Type III aggregations, a compound of types I and II, are shown by adults and juveniles of *Platynothrus peltifer*. A discussion of these results indicates that the Cryptostigmata might have narrower species niches than other arthropods which are either predatory or have active defence mechanisms.

Die Struktur des in einem Kiefernforstboden in Schottland vorkommenden Oribatidenbesatzes (mit 14 Arten) wurde ein Jahr lang untersucht. Es wurde gefunden, daß alle Arten eine starke Tendenz zu einem nesertartigem Vorkommen (aggregierten Verteilung) zeigten. Diese Tendenz ist bei den Cryptostigmata stärker ausgeprägt als bei den anderen Gruppen von Mikroarthropoden, die im gleichen Habitat vorkamen. Einige Arten zeigen jahreszeitliche Unterschiede in der Form ihrer Aggregationen. Eine Untersuchung der Korrelationen zwischen Besatzdichte und der Zahl der Aggregationen oder der Individuendichte in den Aggregationen läßt 3 Distributionstypen der Cryptostigmata erkennen: (I) Arten wie *Camisia spinifer* zeigen, daß die Zahl der Aggregationen mit der Besatzdichte zunimmt. (II) Arten wie *Porobelba spinosa*, *Adoristes poppei*, *Phthiracarus piger* sowie die Adulti von *Ceratoppia bipilis* und *Oribella lanceolata* zeigen, daß die Individuendichte in den Aggregationen mit der Besatzdichte zunimmt. (III) Die Juvenilen und Adulten von *Platynothrus peltifer* zeigen eine Kombination der beiden vorgenannten Verhaltensweisen.

Eine Diskussion dieser Resultate zeigt, daß die Cryptostigmata engere Spezies-Nischen haben als Arthropoden, die entweder Prädatoren sind oder aktive Verteidigungsmechanismen besitzen.

6. Acknowledgements

I should like to thank Dr. D. R. GIFFORD who checked the identification of some of the mites; the Nuffield Foundation for the award of a Biological Bursary and Edinburgh University for the award of a Post-graduate Studentship; and the Forestry Commission for access to the Black Wood of Rannoch.

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